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RELATIONSHIP OF BREEDING BIRD DENSITY AND DIVERSITY TO HABITAT VARIABLES IN FORESTED WETLANDS

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Deciduous forested wetlands are defined as lands dominated by deciduous trees where the water table is at, near, or above the land surface long enough each year to promote the formation of hydric soils, and to support the growth of hydrophytes (Cowardin et al. 1980). This wetland type comprises more than half (75,000 ha) of the total freshwater wetland area in Massachusetts (Golet and Larson 1974) and is common throughout the northeastern U.S.

This study relates breeding bird density and species richness to habitat features in forested wetlands. The basis for relating avian distribution to habitat variables is an hypothesis that physical features may ultimately reflect the suitability of a site for reproduction and survival (Hilden 1965). The distribution and abundance of breeding birds has been related to habitat features in a variety of upland forest types (Anderson and Shugart 1974, Bond 1957, James 1971, Odum 1950, Shugart and James 1973, Smith 1977, and various authors in Smith 1975 and DeGraaf 1978). There has been, however, limited documentation of breeding bird habitat relationships in wetland forest communities, where surface hydrology is a dominant feature affecting the plant and animal community.

METHODS

Study areas.—This research was conducted in eight deciduous forested wetlands, each 30 ha or larger, in the southern half of the Connecticut Valley region of Massachusetts (Fig. 1). Study areas were selected to provide a wide range of vegetation structure, hydrologic patterns, and geographic location.

Quinebaug Swamp was predominantly a shrub swamp with widely spaced young trees in the overstory. Lawrence Swamp and Leadmine Swamp were patchy woodlands with dense stands of sapling to pole-sized trees, mature forest and brushy openings along streams. The other five study areas were more homogeneous, early to late stages of mature red maple forest.

Red maple (*Acer rubrum*) was the most abundant tree species in the overstory of all study areas. American elm (*Ulmus americanus*), yellow birch (*Betula alleghaniensis*), black ash (*Fraxinus nigra*), hemlock (*Tsuga canadensis*), and black gum (*Nyssa sylvatica*) were much less abundant in the canopy layer, but were frequent in young forest stands and as subcanopy trees in mature stands. Several areas had small "islands" of slightly higher elevation occupied by white oak (*Quercus alba*) and white pine (*Pinus strobus*), but these islands were

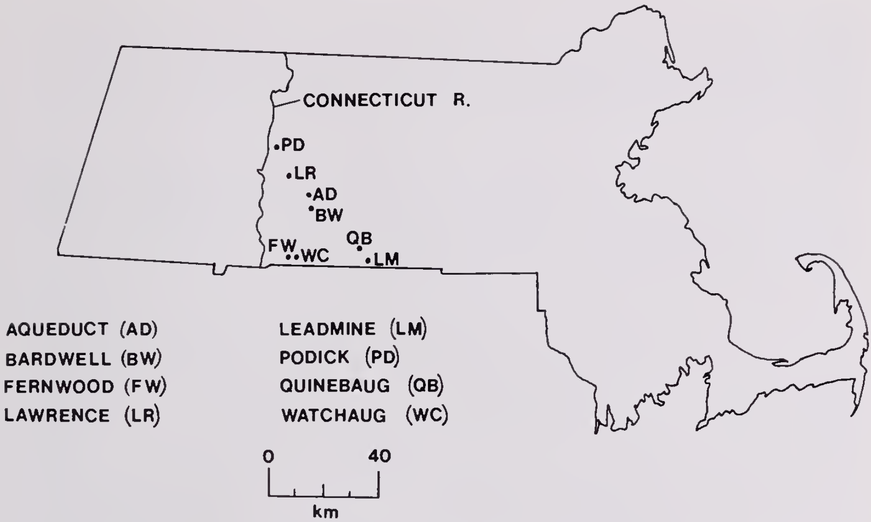

FIG. 1. Names and locations of deciduous forested wetland study areas, Massachusetts.

generally avoided in the selection of census plot locations. Woody plants common in the understory included common winterberry (*Ilex verticillata*), highbush blueberry (*Vaccinium corymbosum*), alder (*Alnus* spp.), arrow-wood (*Viburnum dentatum*), spicebush (*Lindera benzoin*), silky dogwood (*Cornus amomum*), swamp-rose (*Rosa palustris*) and spiraea (*Spiraea* spp.). Cinnamon fern (*Osmunda cinnamonea*), royal fern (*Osmunda regalis*), hummock sedge (*Carex stricta*), skunk cabbage (*Symplocarpus foetidus*), poison ivy (*Toxicodendron radicans*), and sphagnum moss (*Sphagnum* spp.) were common in the herbaceous layer.

Shallow pools of surface water were present on portions of all sites in late May, but disappeared from many during the summer. All study areas showed a seasonal pattern of high water levels in early spring with a drawdown normally occurring into September, depending on rainfall. In 1978, water levels returned to near spring levels by December, exhibiting the annual cycle described by Lyford (1964) for wet forested soils in New England. Plots within each wetland exhibited similar patterns of fluctuation, but range of water table fluctuation was variable among and within most study areas (Swift 1980).

Bird populations.—Data on breeding bird populations were collected on 10 circular 0.25-ha plots (28.2-m radius) within each study area. All plot centers were located at least 100 m from any border with non-hardwood forest cover. Birds were censused on each plot six times per year between 31 May and 30 June, in both 1978 and 1979, between 05:00 and 09:00 EST (when there was no precipitation or strong winds). Each census consisted of a 5-min listening period at a plot center, during which all singing male birds were identified to species and counted. Relative abundance of each species was determined for each plot based on the mean number of singing males observed.

Bird census data were compiled to produce five avian community variables. Total breeding bird density (TBD) was the sum of the relative abundances of all species on a plot. Bird species richness (BSR) was the total number of species observed on a plot during the two breeding seasons. Most species were placed into one of three primary feeding guilds (after Holmes et al. 1979): ground and herb foragers (GRGILD), foilage gleaning birds (FLGILD), and trunk and branch (bark) foragers (BKGILD). The number of birds in each guild was the sum of the relative abundances of the appropriate species. Grouping into guilds was done to identify important habitat components for birds sharing a common foraging substrate.

Habitat measurements.—Analysis of avian habitats was based on measurement and estimation of 15 physical aspects of vegetation and hydrology (moisture regime) at each census plot. Habitat variables included in the study and methods used to measure each are described below. Abbreviations for variables are indicated in parentheses.

Vegetation sampling was conducted on a 0.02-ha area within each census plot during July and August 1978. The sampled area was defined by two perpendicular, rectangular transects (51 × 2 m each), intersecting at the plot center, and oriented in the cardinal directions. Stem counts were divided into size classes as follows: live overstory trees, dbh > 7.7 cm (TREE); subcanopy stems > 5 m in height and dbh ≤ 7.7 cm (SUBCAN); shrub stems 3–5 m in height and dbh ≤ 7.7 cm (TALL); shrub stems 1–3 m in height and dbh ≤ 7.7 cm (SHORT); and standing dead trees, dbh > 7.7 cm (DEAD). Heights of overstory trees were estimated from clinometer readings to determine average height of trees (AVGHGT) and height of the tallest tree (MAXHGT) in the sampled area. Percent crown closure (CROWN) and percent herbaceous cover (HERB) were estimated by noting presence or absence of vegetation in the respective layers at 20 locations along transect center lines. Other vegetation variables were average dbh of overstory trees (DBH) and average height above ground of the lowest live branches on overstory trees (BOLE).

Percent surface "wetness" (WET) was estimated by visually noting presence or absence of surface water at 64 points along the transect center lines. This was done in early June 1978. Presence of streams (STREAM) on plots was noted, and included any channel of flowing water, regardless of size or rate of flow. Depth of muck (SOIL) was measured at all plots by probing with a 0.5 in diameter iron rod to depth of refusal (i.e., where dense mineral soil resisted further penetration), down to a maximum of 2.4 m. This parameter may reflect soil drainage characteristics, since muck soils generally have low vertical permeability (O'Brien 1977).

Water levels were monitored within wells (1.0 m depth × 0.1 m diameter perforated plastic pipe, after Lyford 1964) installed at the center of five census plots in each study area. Measurements were taken concurrently with bird censuses in June 1978 and 1979. During the remainder of the year, data were collected at 4–6 week intervals; all wells were visited within a 36-h period following a minimum of 48 h without precipitation. The magnitude of observed water level fluctuation, i.e., the vertical distance between maximum and minimum recorded water levels (FLUX), was determined for each well. Values for this variable were not estimated for plots that were not monitored.

Quantitative analyses.—Relationships between the five avian community parameters and habitat variables were assessed by multiple regression (ordinary least squares) and simple correlation (Johnston 1972). Data from all plots were used to produce a multiple regression model for each avian community variable. No transformations of data were applied. Water level fluctuation (FLUX) was not included as a habitat variable in the multiple regressions because data were collected from only half of the census plots. Multicollinearity among habitat variables was assessed using additional multiple regressions referred to as "auxiliary regressions" (Johnston 1972). In all analyses, Student's t-test ($P \leq 0.05$) was used to determine significance of the regression coefficient for each habitat variable. F-tests were used to assess the ability of each multiple regression to explain variation of the particular dependent variable.

RESULTS

A total of 2679 observations of singing male birds were recorded, comprising 46 species (Swift 1980). Overall, the most common species were: Common Yellowthroat (*Geothlypis trichas*), Veery (*Catharus fuscescens*), Canada Warbler (*Wilsonia canadensis*), Ovenbird (*Seiurus aurocapillus*), Northern Waterthrush (*S. noveboracensis*), Gray Catbird (*Dumetella carolinensis*), and Black and White Warbler (*Mniotilta varia*). These species accounted for 72% of the observations. While species compositions of study areas were similar, relative abundances and total breeding bird densities were variable.

Estimated densities of birds in the study areas ranged from approximately 132 ± 80 (SD) to 720 ± 113 males per 40 ha (Table 1). Mean density of birds for all areas was 446 ± 195 breeding males per 40 ha. Overall, foliage gleaning birds were the most abundant feeding guild (221 ± 128 males/40 ha), followed by ground feeders (168 ± 88 males/40 ha) and bark gleaners (49 ± 42 males/40 ha). Total number of species observed in the study areas ranged from 15–22, while the mean number of species per plot ranged from 5.5 ± 2.5–10.8 ± 1.9 among study areas.

There were marked differences in habitat characteristics among and within study areas (Table 2). A significant amount of variation in total breeding bird density (TBD), bird species richness (BSR), and abundance of birds in two of the feeding guilds (FLGILD and GRGILD) was explained by habitat variables (Table 3). TBD was positively correlated with small shrub density, surface wetness, and soil depth. BSR was also positively correlated with small shrub density and soil depth, and was inversely related to tall shrub density and height of lowest branches. FLGILD was positively related to surface wetness and soil depth, and was inversely related to percent crown closure. GRGILD was positively related to number of dead trees. No significant results were obtained in the model for bark-foraging species. Extreme multicollinearity was apparent for seven habitat variables which had R^2's > 0.70 (Table 2). This may have precluded the detection of other significant habitat relationships in the multiple regression models.

Results of simple correlations between the avian community parameters and all habitat variables are presented in Table 4. Magnitude of water level fluctuation (FLUX), which ranged from 4–86+ cm, was more highly correlated to TBD, BSR, and FLGILD than was any other habitat variable.

DISCUSSION

Densities and species' richness of breeding birds in this study were generally comparable to those observed in other moist woodlands, such as

TABLE 1

SUMMARY OF BREEDING BIRD CENSUS RESULTS ($\bar{x} \pm$ SD) FOR EIGHT DECIDUOUS FORESTED WETLANDS

Avian variable[a]	Study area[b]								
	AD	BW	FW	TR	LM	PD	QB	WC	ALL
TBD (obs./plot/year)[c]	15.95 ±4.03	14.95 ±3.73	18.05 ±7.43	20.10 ±3.36	19.75 ±2.26	4.95 ±2.99	26.95 ±4.25	13.05 ±4.83	16.72 ±7.29
FLGILD (obs./plot/year)	8.25 ±3.36	5.30 ±2.57	8.05 ±2.82	11.80 ±3.34	10.75 ±1.85	2.00 ±1.24	14.05 ±3.97	5.90 ±4.62	8.26 ±4.81
GRGILD (obs./plot/year)	5.55 ±2.92	6.90 ±1.89	6.05 ±3.78	7.45 ±1.17	5.70 ±1.69	2.30 ±1.27	11.15 ±2.26	5.35 ±2.70	6.31 ±3.31
BKGILD (obs./plot/year)	2.10 ±1.32	2.30 ±1.35	3.55 ±1.80	0.75 ±0.60	3.05 ±1.23	0.35 ±0.59	1.10 ±1.04	1.50 ±0.89	1.84 ±1.57
BSR (no. species/plot)	9.70 ±2.36	8.00 ±2.05	10.60 ±2.95	9.00 ±2.00	9.90 ±0.99	5.50 ±2.46	10.80 ±1.87	8.60 ±1.84	9.00 ±2.60
Total no. species/area	22	19	21	21	18	15	19	22	46

[a] Abbreviations explained in text.
[b] Study area abbreviations explained in Fig. 1.
[c] Density per 40 ha can be computed by multiplying the value by 26.7.

riparian communities, wooded swamps, and cove forests (Brinson et al. 1981). However, the observed significant differences in density and diversity among study areas were not anticipated. This provided an opportunity to closely examine habitat relationships to avian communities in deciduous forested wetlands.

Results of the multiple regressions support an hypothesis that vegetation structure had a significant effect on breeding bird communities in forested wetlands. For example, an increase in number of small shrubs (1–3 m in height) was associated with an increase in both breeding bird density and species richness. The addition of shrubs to the understory would increase structural heterogeneity in a forest, which is believed to be important for providing avian niche diversity (MacArthur and MacArthur 1961, Roth 1976). At the same time, however, the number of tall shrubs (3–5 m) was inversely related to bird species richness. This may suggest that the taller shrubs occupied open space and vertical "edges" that would otherwise have existed between the understory and canopy layers of vegetation; this could affect foraging maneuverability of birds (Balda 1975). The relationship of crown closure to BSR also suggests that openings in the canopy, which would increase structural heterogeneity, enhanced diversity of the bird community. From the data available, it was not possible to hypothesize whether the vegetation variables also reflected differences in site productivity or foliage volume, which have been suggested as possible factors affecting breeding bird communities (Lack 1966, Cody 1974, Willson 1974, Gauthreaux 1978).

Significant correlations were found between the avian community parameters and variables used to quantify hydrologic conditions. These observations may indicate that moisture regime is a basic habitat feature affecting breeding bird communities in forested wetlands. In this study, percent surface wetness and depth of muck were directly related to avian density and species' richness. It appears that the most poorly drained sites had the most abundant and diverse bird populations. This hypothesis was further supported by the inverse correlation between magnitude of water level fluctuation and avian density and species' richness.

The apparent relationship of breeding bird density and diversity to moisture regime may be due to greater understory vegetation and more diverse vegetative structures found in mesic sites (Curtis and Ripley 1975, Dickson 1978). Data collected in this study indicated that percent surface wetness was positively correlated with shrub and subcanopy stem densities (Swift 1980). However, not all moist sites produce a well developed understory. Abundance of understory vegetation in wetland forests may be adversely affected by fluctuating water levels (M. M. Brinson, pers. comm.; Flinchum 1977). In this study, magnitude of water level fluctuation had

TABLE 2

SUMMARY ($\bar{x} \pm SD$) OF HABITAT MEASUREMENTS FOR EIGHT DECIDUOUS FORESTED WETLANDS

Habitat variable[a]	Study area[b]									
	AD	BW	FW	LR	LM	PD	QB	WC	ALL	(R^2)[c]
TREE (no./plot)	13.6 ±6.7	11.6 ±4.5	14.6 ±5.4	15.6 ±5.9	21.3 ±7.5	13.7 ±5.0	11.3 ±5.2	18.5 ±6.5	15.0 ±6.7	0.42
SUBCAN (no./plot)	1.7 ±2.4	1.8 ±2.6	4.2 ±3.1	16.8 ±7.9	9.2 ±6.8	2.6 ±2.2	10.9 ±5.3	2.3 ±3.1	6.2 ±7.0	0.58
TALL (no./plot)	5.7 ±3.9	11.6 ±23.9	11.8 ±5.4	52.1 ±29.1	25.5 ±19.1	4.2 ±3.0	67.4 ±21.3	5.2 ±4.7	22.9 ±28.2	0.82
SHORT (no./plot)	143.1 ±90.9	155.2 ±123.8	165.7 ±64.5	419.1 ±113.5	263.8 ±155.2	67.9 ±23.0	605.9 ±169.6	166.8 ±57.8	248.4 ±200.1	0.87
DEAD (no./plot)	2.6 ±2.7	2.5 ±2.3	4.2 ±2.3	1.0 ±0.9	2.3 ±1.7	2.3 ±2.0	1.5 ±1.3	3.5 ±1.4	2.5 ±2.1	0.26
AVGHGT (m)	14.0 ±2.0	15.6 ±2.3	13.9 ±2.4	10.6 ±1.0	11.9 ±1.5	15.4 ±1.9	7.9 ±1.0	12.9 ±1.3	12.8 ±3.0	0.91
MAXHGT (m)	18.9 ±1.6	19.7 ±2.0	21.1 ±1.4	14.3 ±2.0	16.3 ±2.0	21.9 ±1.9	10.3 ±1.4	17.8 ±2.0	17.5 ±4.0	0.83
BOLE (m)	4.4 ±0.9	5.1 ±1.2	4.9 ±1.2	3.9 ±0.7	5.1 ±0.8	6.1 ±0.8	2.7 ±0.5	4.1 ±0.6	4.5 ±1.3	0.64
DBH (cm)	20.0 ±4.7	21.9 ±4.5	20.3 ±4.3	13.2 ±1.8	15.8 ±2.9	19.0 ±3.4	12.9 ±1.6	18.3 ±3.5	17.7 ±4.7	0.81
CROWN (%)	87.0 ±12.1	94.5 ±4.7	86.0 ±9.4	59.5 ±18.5	83.0 ±12.5	86.0 ±8.0	59.0 ±18.1	94.0 ±3.0	81.1 ±17.8	0.72
HERB (%)	80.5 ±7.9	69.0 ±13.8	79.0 ±10.2	77.0 ±15.4	78.0 ±15.0	74.0 ±14.8	80.5 ±8.2	80.5 ±12.3	77.3 ±13.1	0.20

TABLE 2
CONTINUED

Habitat variable[a]	Study area[b]									(R^2)[c]
	AD	BW	FW	LR	LM	PD	QB	WC	ALL	
WET (%)	29.0	46.6	33.9	59.5	53.0	0.6	65.5	47.8	42.0	0.54
	±27.2	±19.9	±19.6	±10.5	±12.1	±1.8	±7.4	±14.5	±25.1	
STREAM (1/0)	0.0	0.0	0.3	0.5	0.4	0.0	0.1	0.2	0.2	0.24
	±0.0	±0.0	±0.5	±0.5	±0.5	±0.0	±0.3	±0.4	±0.4	
SOIL (cm)	193.9	93.4	170.7	89.6	200.6	41.0	182.8	138.6	138.8	0.36
	±73.9	±56.0	±32.3	±53.4	±48.4	±8.3	±37.2	±82.4	±76.6	
FLUX (cm)	38.0	40.4	30.2	33.6	9.2	71.0	8.2	34.8	33.2	0.83
	±5.7	±14.8	±8.7	±16.6	±3.7	±15.0	±2.6	±14.8	±21.4	

[a] Abbreviations explained in text.
[b] Abbreviations explained in Fig. 1.
[c] Values of R^2 are for the auxiliary regressions relating each habitat variable to all others except FLUX.

TABLE 3

RELATIONSHIPS BETWEEN AVIAN PARAMETERS AND HABITAT VARIABLES DETERMINED BY MULTIPLE REGRESSIONS[a]

Habitat variable	Avian community variables				
	TBD	BSR	FLGILD	GRGILD	BKGILD
Constant	10.270	4.531	5.661	7.083	−1.667
TREE	−0.057	−0.061	0.036	−0.054	−0.016
SUBCAN	−0.026	0.031	0.007	0.001	−0.026
TALL	−0.017	−0.040*	−0.023	−0.005	0.006
SHORT	0.017*	0.007*	0.008	0.008	0.000
DEAD	0.497	0.025	−0.068	0.427*	0.132
AVGHGT	0.791	0.431	0.600	0.119	0.035
MAXHGT	−0.294	0.037	−0.153	0.174	0.029
BOLE	−1.043	−0.747*	−0.276	0.675	−0.062
DBH	0.063	−0.047	−0.650	0.112	0.039
CROWN	−0.080	0.014	−0.108**	−0.001	0.016
HERB	0.008	0.011	0.020	−0.013	−0.001
WET	0.065*	0.012	0.620**	0.005	0.010
STREAM	2.862	1.159	1.529	0.267	0.775
SOIL	0.027**	0.014**	0.018**	0.007	0.002
R^2	0.70**	0.46**	0.72**	0.47**	0.18

[a] Values in the table are multiple regression coefficients for effects of habitat variables, and respective R^2's for the model of each avian variable. Significance levels indicated as follows: * ($P \leq 0.05$); ** ($P \leq 0.01$); df = 66.

a significant inverse correlation with abundance of small shrub stems ($r = -0.64$), tall shrub stems ($r = -0.58$), and subcanopy stems ($r = -0.42$).

The effects of hydrologic patterns on breeding birds in forested wetlands may be greater than the potential influence on vegetation structure. Smith (1977) documented the association of several bird species to vegetation components that corresponded to a more basic preference for positions on the moisture gradient of a forest. In this study, percent surface wetness and depth of muck had significant relationships to avian community variables that were not accounted for by vegetation variables in the multiple regressions. That is, if the vegetation variables remained constant, an increase in breeding bird density (especially foliage gleaners) and species' richness would be expected at sites with deeper organic soils and greater coverage by seasonal surface water. The explanation for these relationships was not determined.

Odum (1950) speculated that higher water content of forests could result in increased bird populations, both directly by providing more available water and moderating temperature changes, and indirectly by producing a more luxuriant vegetation, with greater variety of niches, and perhaps

TABLE 4
SIMPLE CORRELATIONS (*r*) BETWEEN AVIAN COMMUNITY PARAMETERS AND HABITAT VARIABLES[a]

Habitat variable	TBD	BSR	FLGILD	GRGILD	BKGILD
TREE	−0.16	−0.11	−0.02	−0.18	0.04
SUBCAN	0.10	0.31**	0.40**	0.21	−0.22
TALL	0.19	0.57**	0.59**	0.46**	−0.19
SHORT	0.36**	0.68**	0.68**	0.56**	−0.17
DEAD	0.08	0.07	0.21	0.02	0.26*
AVGHGT	−0.23*	−0.52**	−0.53**	−0.45**	0.18
MAXHGT	−0.28*	−0.60**	−0.63**	−0.48**	0.19
BOLE	−0.37**	−0.53**	−0.46**	−0.51**	0.10
DBH	−0.05	−0.31**	−0.39**	−0.20	0.20
CROWN	−0.28*	−0.56**	−0.63**	−0.40**	0.23*
HERB	0.20	0.15	0.17	0.08	−0.01
WET	0.29*	0.57**	0.61**	0.34**	0.03
STREAM	0.27*	0.33**	0.37**	0.12	0.08
SOIL	0.43**	0.45**	0.41**	0.31**	0.16
FLUX[b]	−0.46**	−0.80**	−0.75**	−0.43**	−0.22

[a] Significance levels indicated as follows: * ($P \leq 0.05$); ** ($P \leq 0.01$), df = 78.
[b] df = 38.

a greater amount of food. It is also possible that moisture conditions affect reproduction or distribution of plants and invertebrates (Gaines 1974, Brown et al. 1978), resulting in differences in food availability among structurally similar plant communities. However, these parameters were not analyzed in this study.

Conclusions.—Deciduous forested wetlands appear to be productive habitats for breeding birds. Although forested wetlands usually share a common assemblage of species, total bird density, species' richness and foraging guild structure are significantly affected by components of vegetation structure and hydrology. Analyses of breeding bird habitats should include efforts to quantify and explain the potential effects of moisture regime.

SUMMARY

Breeding bird populations were studied in eight deciduous forested wetlands located in the Connecticut Valley region of Massachusetts. Singing male birds were counted on 10 circular 0.25-ha plots in each study area in June 1978 and 1979. A total of 46 species was observed, with estimated densities varying among study areas from 134–720 males per 40 ha. Avian community parameters (total breeding bird density, bird species richness, and abundance of three foraging guilds) were related to 15 habitat variables by multiple regression

and simple correlation. Results suggested that breeding bird communities in forested wetlands are significantly related to vegetation structure and hydrology. Generally, the most poorly drained sites appeared to have the most abundant and diverse breeding bird populations.

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